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Egg Recognition and Cowbird Egg Ejection Behavior in the American Robin (Turdus migratorius)

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EGG RECOGNITION AND COWBIRD EGG EJECTION BAHAVIOR

IN THE AMERICAN ROBIN (TURDUS MIGRATORIUS)

(TITLE)

BY

ALLISON KARLIEN LANG

THESIS

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Abstract

American Robins (*Turdus migratorius*) typically eject parasitic cowbird eggs from their nests. In order to successfully remove parasitic eggs, robins must first be able to differentiate between their own and foreign eggs and then remove the unwanted egg(s). This study addressed these behaviors. A robin's ability to recognize its own eggs was tested by adding artificial cowbird eggs to robin nests at various parasite-to-host egg ratios which created three treatments: (1) a majority of robin eggs in the nest, (2) an equal number of robin and cowbird eggs, and (3) a majority of cowbird eggs. At 89% of nests (51 of 57), robins ejected all cowbird eggs, and latency to ejection did not differ between these three treatments, indicating egg recognition. However, host-to-parasite egg ratio and date had a significant effect on the risk of ejection: a combination of the likelihood of ejection and latency to ejection. Ejection was more likely to happen, and happen faster, as the proportion of parasitic eggs in the nest increase and as the nesting season progressed. Because the likelihood of birds undergoing their initial nesting attempt is greater earlier in the nesting season, these results suggest that robins may learn to recognize their own eggs during their initial nesting attempt.

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Introduction

Brown-headed cowbirds (*Molothrus ater*; hereafter cowbirds) are a ubiquitous brood parasite, laying their eggs in the nests of many passerine species in North America (Friedman and Kiff 1985). Such parasitism typically reduces a host's reproductive success (Rothstein 1975a, Payne 1977, May and Robinson 1985, Airola 1986, Lorenzana and Sealy 1999). As a result, many host species have developed behaviors which minimize the success of cowbird parasitism (Rothstein 1990). These behavioral adaptations include increased nest defense during egg-laying, cowbird egg rejection, or nest abandonment after a cowbird egg has been laid (Robertson and Norman 1976).

Many potential host species have been categorized as either "acceptor" or "rejecter" species (Rothstein1975b, Friedmann et al. 1977); all (or nearly all) individuals of a given species react in the same way to cowbird parasitism (Rothstein 1975b). Whereas acceptor species typically incubate cowbird eggs, rejecter species reject cowbird eggs from their nest in various ways. Most commonly, rejecters remove the parasitic egg from their nest completely, which has been termed "ejection" (Rothstein 1975b).

American Robins (*Turdus migratorius*; hereafter robins) are categorized as cowbird egg rejecters (Rothstein 1975b, 1982). Many previous studies (Friedmann et al. 1977, Rothstein1975a, 1975b, Rassmussen et al. 2009) have verified that robins are a rejecter species, with little intraspecific variation (Rothstein 1975a). Eggs are most often ejected by grasping the egg with their bill, but robins have also been known to eject eggs by pecking at the foreign eggs despite the risk of damage to their own eggs (Rasmussen et al. 2009).

To eject a parasitic egg from its nest, the robin must be able to recognize which egg(s) should be ejected. Rothstein (1982) suggested that robins are able to recognize differences between cowbird eggs and their own eggs through visual inspection, based on the fact that robin eggs differ from cowbird eggs in both size and coloration (Rothstein 1978). Also, Rensch (1925), and then Rothstein (1975b) identified two possible modes of recognition: true egg recognition whereby robins are able to identify their own eggs because of visual differences between their eggs and cowbird eggs, or "recognition by discordancy" whereby robins eject the egg type found in the minority; which is most often the parasitic egg type.

For a successful ejection, both recognition of a bird's own eggs and removal of foreign eggs are necessary. Thus, egg recognition and ejection are related, but separate behaviors.

Imprinting has been suggested as the mechanism by which ejector species such as robins learn to recognize their own eggs (Strausberger and Rothstein 2009). This imprinting occurs only once during a bird's first nesting attempt, but could be refined through successive nesting attempts (Rothstein 1974, 1978). Rothstein (1975a) found support for the development of egg recognition through imprinting in grey catbirds *(Dumetella carolinensis)* that showed greater tolerance for cowbird eggs earlier in the nesting cycle. "Own egg" recognition as a result of imprinting was further supported by Strausberger and Rothstein (2009) when several rejecter species misimprinted on cowbird eggs when they had laid only one egg of their own.

This study addressed egg recognition behavior of robins and the trends in ejection behavior with relation to both date during the nesting season and degree of cowbird parasitism. First, I hypothesize that robins display true egg recognition (and not recognition by discordancy) and learn to recognize their own eggs during their first nest attempt (possibly through some form of imprinting). If this is true, I would expect robins to recognize and eject all cowbird eggs placed in their nest regardless of the ratio at which they are applied. Second, I hypothesize that the behavior of egg ejection develops over the first nesting cycle as a bird gains experience and learns to recognize its own eggs. I expect that experienced birds will express ejection behavior but that naïve birds tending their first nest might have more difficulty successfully ejecting cowbird eggs from their nest. If there is a difference in the expression of ejection behavior between naïve and experienced birds, there should be a seasonal increase in ejection behavior reflecting the higher proportion of naïve birds nesting at the beginning of the season.

Both of these hypotheses were tested in a two part study. In the first, the ratio of cowbird-to-robin eggs was experimentally manipulated in naturally occurring nests. By using a wide range of parasite-to-host egg ratios across several months of the nesting season, I tested how egg ratio affected recognition and how period of the nesting season affected a robin's ability to successfully eject artificial cowbird eggs from its nest. The second part of the study used a video recording system to obtain more specific observations of ejection behaviors exhibited by American Robins.

Methods

Artificial eggs mimicking those of both Brown-headed Cowbirds and American Robins were hand-formed from modeling clay (Sculpey Original®) and then baked (Bayne and Hobson 1999). Artificial cowbird eggs averaged 22.2±0.33 x 16.9±0.52 mm (subsample N=20), compared to real cowbird eggs at 21.5 x 16.2 mm (Bent 1958). Artificial robin eggs averaged 29.5±0.50 x 21.7±0.67mm (subsample N=7) in comparison to real counterparts with measurements of 28.1 x 20.0 mm (Bent 1949). All eggs were painted with acrylic all-purpose water-based paint (DecoArt®) and sprayed with a clear acrylic gloss (Krylon Indoor/Outdoor®). This acrylic paint and gloss allowed me to easily detect pecking on the surface of the egg.

Nests were found in parks, campuses, and other suburban areas in both Charleston and Mattoon, Illinois (Coles County) during May and June of 2010 (N=44) and April of 2011 (N=27). All nest areas were tested only once per year to avoid testing the same birds more than once. Also, because robins tend to return to the same nesting location each year (Young 1955), different locations within the study area were used each year. Every nest was assigned a Julian day for the initial day the manipulation occurred. This allowed me to combine both years of data for analysis and thereby assess potential effects of the period of the nesting season. The first nest found at the start of the study was randomly assigned a treatment of "majority robin," "equal," or "majority cowbird." After our manipulations, "majority robin" nests had more robin eggs than cowbird eggs, nests in the equal treatment group had an equal number of cowbird and robin eggs, and majority cowbird nests had more cowbird eggs than robin eggs. All subsequent nests were assigned a treatment sequentially. To allow robins the opportunity to learn to recognize their own eggs, only nests that contained at least two eggs were used in our manipulations.

When manipulating nests, the assigned treatment and number of eggs found in the nest determined the exact manipulation. To mimic a natural parasitism event as closely as possible, the total number of eggs in the nest was never increased by more than one. As the number of eggs initially found in a nest was variable, the number of robin eggs removed and the number of cowbird eggs added varied accordingly; more than one robin egg was removed in many cases to achieve the desired ratio. For example, if a nest assigned a "majority cowbird" treatment was found with three robin eggs initially, 3 cowbird eggs would replace 2 of the robin eggs. After manipulation, the total number of eggs would have been increased from 3 to 4, and the resulting ratio would be 3 cowbird eggs to 1 robin egg. If that same nest was given the "equal" treatment, one robin egg would be removed and two cowbird eggs would be added, resulting in two robin and two cowbird eggs after manipulation. As a control, artificial robin eggs were added to 8 other nests by replacing one real robin egg with one artificial robin egg without adding any artificial cowbird eggs.

After manipulation, nests were checked at approximately 24 hour intervals for five days. Nests that still contained cowbird eggs on the fifth day were considered to have "accepted" the parasitism (Rothstein 1975a).

A motion detecting color video camera was used to observe the initial response to cowbird parasitism at two robin nests during the 2011 nesting season. One clay cowbird egg was added to each nest and the camera was attached to a nearby branch or trunk approximately 30 cm above the nest. The camera was left to record for approximately five hours.

We conducted two separate survival analyses using either treatment egg ratio or Julian day as the independent variable. In this context, survival analyses combine the likelihood that an ejection occurred and the latency to that ejection, together represented by a hazard ratio (Bayne and Hobson 1999). The hazard ratio is an estimate of the risk of ejection in response to a predictor variable. This risk estimate will be hereafter referred to as risk of ejection.

Robins exhibited one of four responses to the eggs placed in their nest: 1.) all parasitic eggs were removed, 2.) all parasitic eggs were pecked but not removed, 3.) some (but not all) parasitic eggs were pecked but not removed, or 4.) no eggs were pecked or removed. I separate these four responses into three categories: full ejections (no. 1 above), partial ejections (2 and 3), and no ejection (no. 4). Robins that removed cowbird eggs from their nests were termed full ejections. Alternatively, if eggs were not removed but peck marks were observed, the nest was termed a partial ejection. While both partial and full ejections were included in the survival analysis, only the nests that fully ejected cowbird eggs were analyzed using a Kruskal Wallis analysis to assess the effect of treatment ratio (number of cowbird eggs per robin egg), overall treatment (majority cowbird, equal, majority robin), and the number of eggs present at the start on manipulation on the number of days to ejection. The number of days to ejection was used to assess the ability of robins to recognize foreign eggs, and the ability to remove foreign eggs from their nest. This was based on the assumption that the latency to ejection is correlated with the birds' ability to recognize and remove foreign eggs. If ratio affects this ability, there will be varying response times, influenced by differential ability to recognize and eject cowbird eggs.

Results

A total of 71 robin nests were found and manipulated during 2010 and 2011. Of these, 57 were included in my analyses. Fourteen nests were removed from analysis because of depredation, abandonment, or hatching of robin eggs within the five day observation period. First, if all of the eggs (both robin and cowbird) were removed within the five day observation period, I assumed that the nest was depredated (N=3). This was assumed because predators typically remove all eggs from the nest (Rothstein 1975b). Second, five nests were abandoned immediately prior to manipulation or very soon thereafter. It is unlikely that our manipulation of nest contents caused these desertions (Rothstein 1975b); it is also unlikely that robins would desert their nest in response to cowbird parasitism (Rothstein 1975a). It is more likely that desertions occurred because of weather or other natural events and, therefore, I did not include these nests in our analyses. Finally, eggs hatched in six of the nests during the 5 day observation period. As these nests were no longer in the incubation stage of the nesting cycle, they were removed from the analysis (Rothstein 1975b).

Of the 57 nests in my analysis, 51 fully ejected their cowbird eggs (89.5%). In four of the six nests that did not fully eject cowbird eggs, peck marks were observed on at least one egg in the nest. However, two nests subjected to the equal treatment did not show any damage to the cowbird eggs by the fifth day. The four nests that showed some evidence of pecking were in either the "majority robin" or "majority cowbird" treatments.

Three robin nests had fewer robin eggs after the artificial cowbird eggs were ejected, indicating that the host bird may have damaged their own eggs while trying to eject the parasitic eggs. Two of the three nests were missing one egg, while the bird tending the third nest may have damaged both of its eggs in the process of removing the cowbird egg. The own-egg damage rate in these nests were 33%, 50%, and 100%, respectively.

Across all treatments, 66.7% of ejections occurred within the first 24 hours of manipulation (Figure 1). For nests that fully ejected all cowbird eggs, there was no difference in the days to ejection among parasite-to-host egg ratios (Chi-square=4.87; 6 df; P=0.56; Table 2), nor among treatment groups (Chi-square=3.87; 2 df; P=0.14; Table 2). The number of robin eggs present in the nest at time on manipulation also had no effect on the latency to ejection (Chi-square=4.31; 2 df; P=0.12). The likelihood of ejection occurring and the latency to ejection were combined as the risk incurred by a cowbird egg using a survival analysis. This risk increased with time into the nesting season (using the Julian day of manipulation, Chi-square = 4.96; 1 df; P=0.03), where birds tending nests later in the season were more likely to eject and eject faster. Also, risk increased with the number of cowbird eggs present in the nest (Chi-square = 6.21; 1 df; P=0.01).

Video recordings of two nests showed variation in response to the cowbird egg. At the first nest (12 May 2011), the adult robin returned to the nest within 2 minutes and 30 seconds of the manipulation. Upon its arrival, the robin began pecking at the artificial egg that had been placed in the nest. This continued for 45 seconds, at which time the robin flew away and then returned in 6 seconds to grasp the egg in its bill and fly away with it. The second nest was manipulated and recorded in the same way approximately 24 h later. At this nest, the adult took slightly longer to return to the nest (3 min), and began pecking at the cowbird egg less vigorously. Instead of removing it, the bird pecked several times and then settled in to incubate the eggs. This process happened six times throughout the recording period every time the bird returned to the nest. At one point both adults perched on the edge of the nest and pecked alternately, and one even opened its bill in what seemed to be an attempt to grasp the egg. Ultimately, however, they did not remove the artificial cowbird egg but continued with incubation. The cowbird egg was still in the nest after approximately 5 hours when the video camera was removed. Finally, all eight artificial robin eggs remained in the nest with no evidence of pecking for five days.

Discussion

If robins are able to recognize their own egg type, the ratio of egg types should have no affect on the bird's ability to eject foreign eggs. My results support this hypothesis: robins were typically able to recognize their own eggs regardless of host-to-parasite egg ratio. In only two nests (of 57) did adults not eject or peck at at least one of the cowbird eggs.

Evidence of egg recognition was also seen at both nests where I video recorded post-manipulation behaviors displayed by the host birds. One nest ejected while the other pair of birds pecked at the cowbird egg repeatedly (but not their own eggs), indicating recognition of the cowbird egg as foreign to the nest. Recording at the first nest showed the bird pecking at the artificial cowbird egg prior to grasping and ejecting it. This may be a form of exploratory pecking whereby birds are inspecting the foreign egg, or variation in ejection behavior. Consistent with the findings of Rothstein (1975b), these results occurred regardless of treatment ratio of eggs.

The lack of pecking on some but not all artificial cowbird eggs at four nests might be due to the artificiality of the eggs. If pecking at the first egg did not result in it breaking, the robin may have been discouraged from attempting to destroy the other artificial parasitic eggs. These nests are considered partial ejections because, while the birds did not remove the cowbird eggs from their nest, peck marks suggest recognition of a foreign egg. Previous studies (Rothstein 1975a, 1975b, 1982) which only added a single artificial cowbird egg to nests have treated peck marks as ejections, but my study differs in that more than one cowbird egg was added to the majority of nests in order to achieve the desired treatment ratios. In doing so, robins were exposed to more than one egg, allowing me to observe their response to multiple foreign eggs.

While recognition was exhibited by nearly all of the birds, not all that recognized their own eggs also ejected the cowbird eggs. The lack of ejection by all birds that recognized the foreign eggs suggests that pecking might be a response to a foreign object in the nest, and that ejection behavior (through grasping the egg) may develop progressively beyond this initial recognition of foreign eggs. On the other hand, some robins may be puncture ejectors and others may be grasp ejectors like Rasmussen et al. found for catbirds (2009).

The development of ejection behavior in first-time nesters was assessed using the effect of date during the nesting season on ejection. Correctly differentiating yearling from adult American Robins is difficult and we did not capture adults (Howell 1942). Therefore, the number of days into the nesting season was used as an alternative method of assessing the experience level of birds. While older birds are known to breed earliest (Klomp 1970), I expected that a greater number of naïve birds (i.e., first-time nesters) would nest earlier in the season, resulting in the highest proportion of first time nesters earlier in the nesting season. My results supported the development of ejection behavior over time. The statistically significant effect of date on the risk of ejection suggested that earlier in the nesting season, birds were less likely to eject cowbird eggs, and if ejection occurred, birds took longer to do it. That the date had an effect on the risk of ejection could be explained by a higher proportion of birds nesting for the first time earlier in the nesting season. It is these birds that might have yet to fully develop ejection behavior and be less likely to eject cowbird eggs from their nests.

I may have only observed full ejections later in the breeding season because birds that were nesting for the first time at the beginning of the season had moved on to their second (and maybe third) nesting attempts. Along with general nesting experience, I would expect learning to recognize the eggs present in their nest to continue. My study allowed for some initial learning of own egg type to take place, but this would most likely continue over the first nesting attempt, and with increased experience, ejection rates would be expected to increase over the nesting season.

In my study, the variation in response to cowbird eggs was also affected by the parasite-to-host egg ratio present in the nest. As the number of cowbird eggs increased, the risk of ejection also increased. Previous studies have considered foreign eggs as a stimulus for nest cleaning behavior, which could be a preadaptation for egg ejection (Rothstein 1975a; Moskat et al. 2003). This suggests that the stimulus of the egg elicits a potentially innate removal response. Also, as a stimulus that elicits a behavioral response, multiple foreign eggs in a robin's nest might be an example of a supernormal stimulus, where an increase in the stimulus increases the intensity of the reaction (Tinbergen 1948). Such a stimulus causes animals to show greater responsiveness to stimuli that differ substantially from their own: in this case multiple cowbird eggs in their nest (Staddon 1975).

I suggest that ejection behavior develops as robins gain nesting experience and increased exposure to their own eggs. Later in the nesting season I found higher rates of ejection, presumably after birds had fully learned to recognize on their own eggs and had developed the ability to eject foreign eggs. Rothstein (1974) found support for the idea that learning continues to refine recognition behavior throughout the nesting cycle, but could not identify a period when the learning process occurs. While imprinting may begin on the first few eggs, robins may require a longer period or additional eggs to fully imprint. A developmental period might exist during a bird's first nesting attempt whereby naïve birds imprint on their own eggs and develop ejection behavior, and if presented with foreign eggs during this period, young birds do not fully express ejection behavior.

Because the proportion of intermediate rejections (pecking without removal) seen in this study was so low, it might suggest that full imprinting and development of ejection behavior occurs within the first nesting attempt and is carried over to the next nesting season. Once recognition and ejection behaviors have developed, robins are not affected by the number of cowbird eggs in their nest, nor the portion of incubation during which they are parasitized.

My results also indicate that once developed, ejection behavior is permanent; further evidence for ejection as an innate, but progressively developed, behavior. When considering only the birds that ejected all cowbird eggs, days to ejection did not differ between parasite-to-host egg ratios or treatment groups. Also, date was not significantly related to the latency to ejection for birds that fully ejected foreign eggs. Because neither ratio, nor period of the nesting season had an effect on latency to ejection for "full-ejectors," I suggest that these birds can both identify their own eggs and successfully remove them from their nests.

Based primarily on evidence that birds imprint on the first eggs in their nest, egg recognition has long been considered a learned trait (Rothstein 1974). My study supports recognition by imprinting and that egg ejection is not always an immediate response to foreign eggs, but may require a development period during the first nesting attempt to be fully expressed. This study has shown that a large majority of American robins tested recognized the foreign eggs in their nest, but not all had developed the grasp-ejection behavior normally exhibited by this species.

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Tables

Table 1. Outcomes at the four partial ejection nests from which cowbird eggs were not removed and two nests where artificial cowbird eggs were accepted.

1st Egg Date	Parasite-to-Host Egg Ratio	Presence of Pecking	Notes
21-April	2:3	Yes	1 of 2 cowbird eggs pecked on 2nd day
21-April	3:2	Yes	2 of 3 cowbird eggs pecked on 2nd day
26-April	2:2	No	
26-April	2:2	No	
28-April	2:3	Yes	1 of 2 cowbird eggs pecked on 3rd day
28-April	1:2	Yes	1 of 1 cowbird egg pecked on 3rd day

Table 2. Summary of the latency to ejection by treatment ratio (Chi-square=4.87; 6 df; P=0.56) and treatment group (Chi-square=3.87; 2 df; P=0.14).

Parasite-to-Host Egg Ratio	Average Days to Ejection	SD	N
1:3	1.33	0.82	6
1:2	2.33	0.58	3
2:3	1.50	0.71	10
1:1 & 2:2	1.67	1.12	9
3:2	1.00	0.00	8
2:1	1.40	0.55	5
3:1	1.60	0.97	10
Treatment Group			
Majority Robin	1.58	0.77	19
Equal	1.67	1.12	9
Majority Cowbird	1.35	0.71	23

Figures

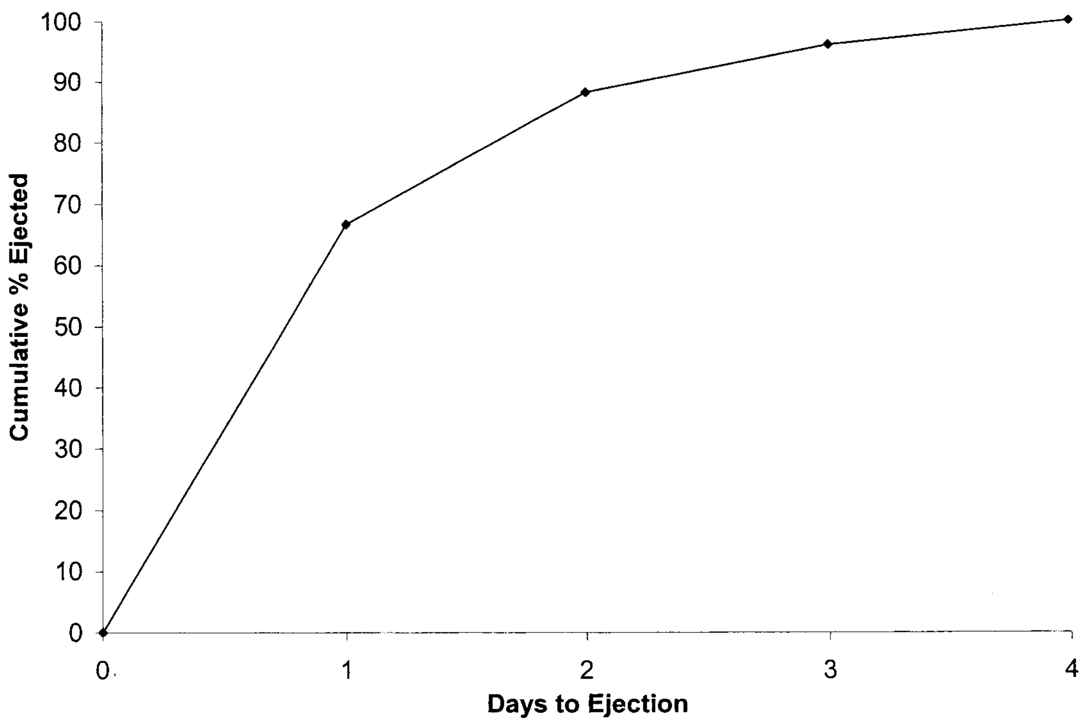

Figure 1. Latency to ejection of artificial cowbird eggs placed in 57 American robin nests.